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– PROCEEDINGS –

CONGRESSUS EUROPAEUS ICHTHYOLOGORUM

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SVEN O KULLANDER BO FERNHOLM

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Contents

Papers presented to the Symposium on Antarctic Fish Biology

The hypothalamic, ventricular channel-system and its phylogenetic distribution among fishes

MARIO F. WULLIMANN
University of Michigan, Ann Arbor, Michigan, USA

Wullimann, M.F. 1987. The hypothalamic, ventricular channel-system and its phylogenetic distribution among fishes. *Proc. V Congr. europ. Ichthyol., Stockholm 1985, pp. 65–72.* The inferior lobes, bilateral diverticuli of the ventral hypothalamus, characterize both cartilaginous and ray-finned fishes but are not found in lobe-finned fishes (coelacanths and dipnoans) or in tetrapods. In the Picasso trigger fish, *Rhinecanthus aculeatus* Linnaeus (Balistidae), the lateral recess of the third ventricle, which protrudes into the inferior lobes, displays a peculiar series of channels, with pores leading to the outside of the brain. In order to determine the evolutionary polarity of this neuroanatomical feature, series of transverse brain sections from members of all major groups of fishes were examined for the presence of such a channel-system (11 chondrichthyans, 2 cladistians, 3 chondrosteans, 1 ginglymode, 1 halecomorph, 58 teleosteans). This feature appears to have originated only with the Clupeocephala of Lauder and Liem, and its fully developed state is restricted to the Percomorpha, specifically balistids (Tetraodontiformes) and pomacentrids, cichlids and labrids (Perciformes). Therefore, this feature most likely represents an apomorphic neural character within actinopterygian fishes.
Division of Biological Sciences, University of Michigan, Ann Arbor, Michigan 48109-1048, USA.

Unlike in land vertebrates, the hypothalamus is the most highly differentiated part of the diencephalon in fishes. One of the most extensive hypothalamic specializations is the inferior lobes (Fig. 1). These bilateral diverticuli of the ventral hypothalamus characterize both cartilaginous and ray-finned fishes but are not found in lobe-finned fishes (coelacanths and dipnoans) or in tetrapods. In some species of cartilaginous and ray-finned fishes, the relative size of these ventrolateral hypothalamic brain parts is comparable to that of other major brain divisions, such as the cerebellum or the optic tectum (Fig. 1).

A particulary striking feature of the inferior lobes in the Picasso trigger fish, *Rhinecanthus aculeatus* Linnaeus is the presence of a ventricular, hypothalamic channel-system (Wullimann *et al.* 1984). In order to determine the phylogenetic distribution and evolutionary polarity (plesiomorphy versus apomorphy) of this neural character, members of all major fish groups were examined for its presence. These data were then examined for possible correlations with the ecology and behavior of the fishes exhibiting a ventricular, hypothalamic channel-system. As fishes constitute the largest and most variable group of vertebrates, the comparative approach, emphasized in this study, is the most appropriate method for elucidating the biological role of the inferior lobes, a role which is still essentially unknown.

There is a great deal of information available on the inferior lobes, including their overall morphology (Holmgren 1920, Bergquist 1932, Ariëns Kappers *et al.* 1936, Crosby & Showers 1969, Demski *et al.* 1975, Evan *et al.* 1976, 1976*a*, Kuhlenbeck 1977, Senn 1981, Wullimann *et al.* 1984), their neuronal connections (Luiten & Van der Pers 1977, Finger 1978, 1983, Morita *et al.* 1980, Sakamoto & Ito 1982, Smeets & Boord 1985), their histology (Knowles 1972, Demski *et al.* 1975, Evan *et al.* 1976, 1976*a*), their ultrastructure (Vigh & Vigh-Teichmann 1973, Kriebel 1982) and their histochemistry (Baumgarten & Braak 1967, Braak 1967, Vigh-Teichmann *et al.* 1970, Parent *et al.* 1978, Parent 1979, 1983, Parent & Northcutt 1982, Halpern-Sebold & Schreibmann 1983, Kotrschal & Adam 1983, Vigh-Teichmann *et al.* 1983, Ekström & Van Veen 1984, Ekström *et al.* 1985, Margolis-Kazan *et al.* 1985). Only a few behavioral and physiological studies (Demski & Knigge 1971, Demski 1973, 1981, 1983, Peter 1979), however, have dealt with the functional aspects of these brain parts.

I would like to express my gratitude to R. Glenn Northcutt and David G. Senn for offering access to their large collections of brain series, to William L. Fink and the Museum of Zoology, University of Michigan, and Toni Bürgin for providing brains of additional specimens included in this study, to Mary Sue and R. Glenn Northcutt for extensive help in preparing the manuscript and innumerable other support, and to Rosemarie Daetwyler and David Bay for technical help. This study was supported by the Janngen–Poehn–Stiftung, Switzerland, and by National Institutes of Health research grant NS11006, USA.

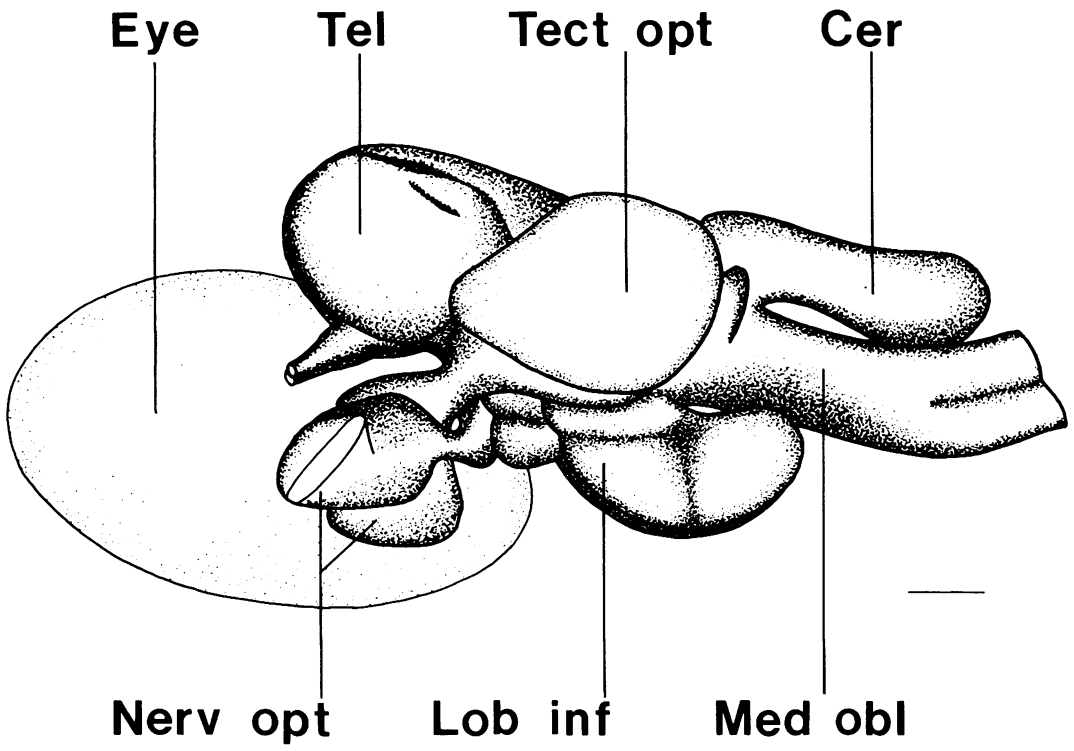

Figure 1. Reconstructed lateral view of the brain of *Rhinecanthus aculeatus* showing the relative size of the inferior lobes compared to other brain divisions. The cranial nerves were omitted, the white structure in the left optic nerve is the optic papilla. Cer, corpus cerebelli; Lob inf, lobus inferior; Med obl, medulla oblongata; nerv opt, nervus opticus; Tect opt, tectum opticum; Tel, telencephalon. Bar scale equals 1 mm.

Table 1. *The phylogenetic distribution of the hypothalamic, ventricular channel-system among fishes (Systematics: after Lauder & Liem 1983, except Chondrichthyes: after Nelson 1976. P: lateral recess leads to periphery of inferior lobe, C: presence of ventricular channels).*

Systematic group			P	C
CHONDRICHTHYES:				
Squalus acanthias	Squalidae	Squaliformes	–	–
Isistius brasiliensis			–	–
Squatina dumeril	Squatinidae		–	–
Heterodontus francisci	Heterodontidae	Heterodontiformes	–	–
Gynglimostoma cirratum	Orectolobidae	Lamniformes	–	–
Mustelus canis	Carcharhinidae		–	–
Notorhynchus maculatus	Hexanchidae	Hexanchiformes	–	–
Raja eglanteria	Rajidae	Rajiformes	–	–
Platyrhinoidis triseriata	Rhinobatidae		–	–
Urolophus sp.	Dasyatidae		–	–
Hydrolagus colliei	Chimaeridae	Chimaeriformes	–	–
OSTEICHTHYES:				
Cladistians				
Polypterus palmas	Polypteridae	no order	–	–
Erpetoichthys calabaricus			–	–
Chondrosteans				
Acipenser oxyrhynchus	Acipenseridae	no order	–	–
Scaphirhynchus platorhynchus			–	–

Polyodon spathula	Polyodontidae	no order	–	–
Ginglymodes				
Lepisosteus osseus	Lepisosteidae	no order	–	–
Halecomorphs				
Amia calva	Amiidae	no order	–	–
Teleosteans				
Osteoglossomorpha				
Osteoglossum bicirrhosum	Osteoglossidae	Osteoglossoidei	–	–
Pantodon buchholzi			–	–
Xenomystus nigri	Notopteridae	Notopteroidei	–	–
Gnathonemus petersi	Mormyridae		–	–
Hiodon tergisus	Hiodontidae		–	–
Elopomorpha				
Elops saurus	Elopidae	no order	–	–
Anguilla anguilla	Anguillidae	Anguilliformes	–	–
Gymnothorax moringa	Muraenidae		–	–
Clupeomorpha				
Clupea harengus	Clupeidae	Clupeoidei	–	+
Brevoortia tyrranus			–	+
Engraulis mordax	Engraulidae		–	+
Euteleostei				
Esox lucius	Esocidae	Esocae	–	–
Umbra limi	Umbridae		–	–
Salmo trutta	Salmonidae	no order	–	–
Salmo gairdneri			–	–
Ostariophysans				
Carassius auratus	Cyprinidae	Cypriniformes	–	–
Crenuchus spilurus	Characidae	Characiformes	–	–
Ictalurus punctatus	Ictaluridae	Siluriformes	–	+
Ictalurus melas			–	+
Sorubim lima	Pimelodidae		+	–
Gymnotid species	Gymnotidae		–	–
Neoteleostei				
Trisopterus minutus	Gadidae	Gadiformes	–	–
Atherinomorpha				
Leuresthes tenuis	Atherinidae	'Atherinoids'	+	–
Poecilia reticulata	Poeciliidae	Cyprinodontiformes	+	–
Strongylura notata	Belonidae	Beloniformes	+	–
Percomorpha				
Hippocampus zosterae	Syngnathidae	Gasterosteiformes	+	–
Holocentrus spinifer	Holocentridae	Beryciformes	–	–
Anthias squamipinnis	Serranidae	Perciformes	–	–
Lepomis gibbosus	Centrarchidae	Percoidei	–	–
Lepomis cyanellus			–	+
Toxotes jaculatrix	Toxotidae		+	–
Trachinotus falcatus	Carangidae		?	+
Lipogramma klayi	Grammidae		–	–
Amphiprion sp.	Pomacentridae	Labroidei	+	+
Dascyllus aruanus			+	+
Chromis chromis			–	+
Astronotus ocellatus	Cichlidae		+	+
Oreochromis mossambicus			+	+
Hemichromis bimaculatus			+	–
Cichlasoma erythraeum			?	+
Embiotoca jacksoni	Embiotocidae		+	?
Cymatogaster aggregata			+	–
Labroides dimidiatus	Labridae		+	+
Coris julis			+	+
Astroscopus y-graecum	Uranoscopidae	Blennioidei	–	–
Gobius niger	Gobiidae	Gobioidei	–	–
Mistichthys accuminatus			–	–
Sphyraena barracuda	Sphyraenidae	Sphyraenoidei	–	+
Anabas testudineus	Anabantidae	Anabantoidei	–	–
Betta splendens	Belontiidae		–	–
Scorpaena porcus	Scorpaenidae	Scorpaeniformes	–	–
Ophicephalus africanus	'Channidae'	Channiformes	–	–
Rhinecanthus aculeatus	Balistidae	Tetraodontiformes	+	+
Odonus niger			+	+
Melichthys vidua			+	+
Diodon hystrix	Diodontidae		–	–
Buglossidium luteum	Soleidae	Pleuronectiformes	–	–
Lepidopsetta bilineata			?	+

Materials and Methods

Brains of all 76 species listed in Table 1 were fixed in AFA (90 ml 80% ethanol, 5 ml stock formaldehyde, 5 ml glacial acetic acid), embedded in paraffin and sectioned at 15 μm. Series of transverse or sagittal sections were then impregnated with Bodian-silver and/or stained with cresyl-violet (modification of Senn 1966).

The reconstruction of the lateral view of the brain (Fig. 1) was done using a Wild-M5 drawing tube. Photomicrographs (Figs 2 & 3) of combined Bodian-cresyl material were taken using a Zeiss photomicroscope and Agfapan 25 film.

Results

In actinopterygians the third ventricle protrudes bilaterally into the inferior lobes, forming the lateral recess, in one of two very distinct morphological patterns. In the first, the lateral recess displays a peculiar series of channels, with pores leading to the outside of the brain, as exist in the Picasso trigger fish, *Rhinecanthus aculeatus* (Fig. 2).

We have postulated that these channels are part of a functional unit, possibly involved in hormone production, in concert with blood vessels, connective tissue and bone structures in that area (Wullimann *et al.* 1984). A dense venous network, located in a pouch at the base of the cranium, underlies the meninx primitiva exactly in the region of the channel openings.

The lateral recess of the inferior lobe in most teleosts exhibits a second pattern, in which there are no channels leading to the external surface of the brain. This condition is seen in *Esox lucius* (Fig. 3).

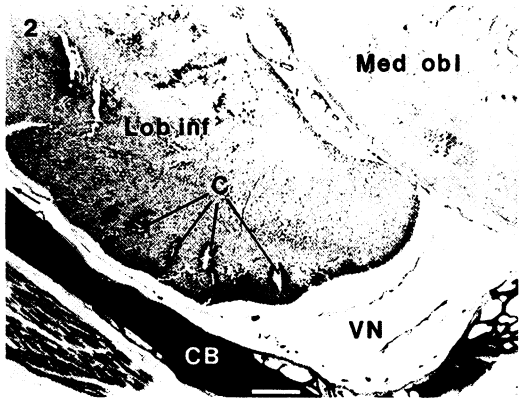

Figure 2. Parasagittal section of the inferior lobe (lob inf) of *Rhinecanthus aculeatus* showing the ventricular channels (C) and the venous network (VN) which is located in a pouch of the cranial base (CB). Med obl, medulla oblongata; arrow points rostrally; bar scale equals 0.2 mm.

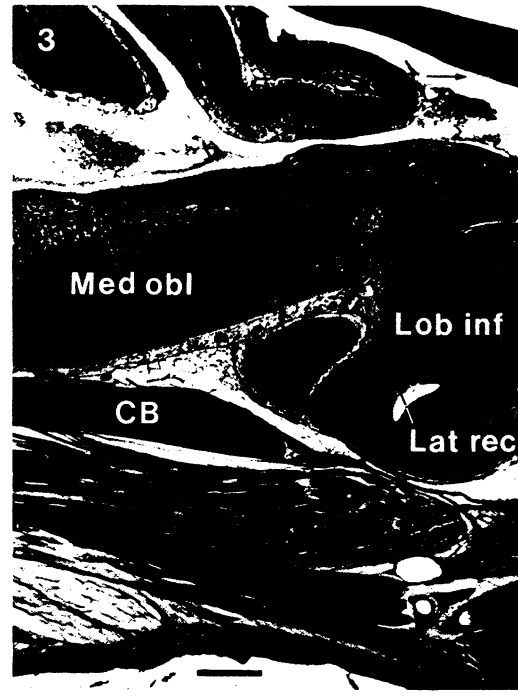

Figure 3. Parasagittal section of the inferior lobe (lob inf) of *Esox lucius*. The lateral recess (lat rec) shows no ventricular channels, and the cranial base (CB) does not form a pouch which would allow the development of a venous network. The rest of the abbreviations are the same as in Fig. 2. Bar scale equals 0.2 mm.

In order to obtain an overview of the morphological diversity and phylogenetic distribution of the modes of contact between the lateral recess of the inferior lobe and the external surface of the brain, a variety of species were examined (Table 1) for the existence of ventricular channels leading to the medio-ventral periphery of the inferior lobe (C in Table 1) and for the presence of a lateral recess leading to the medio-ventral periphery of the inferior lobe (P in Table 1). The results of this survey are listed in Table 1.

In total, 76 species were studied (11 chondrichthyans, 2 cladistians, 3 chondrosteans, 1 ginglymode, 1 halecomorph and 58 teleosts). The neuroanatomical feature comprising the pattern seen in *Rhinecanthus aculeatus* seems to have originated only with the Clupeocephala (Clupeomorpha and Euteleostei) of Lauder & Liem (1983), and it is fully expressed (i.e. the lateral recess leads to the periphery of the inferior lobe as do its channels) only in the Percomorpha, specifically balistids (Tetraodontiformes) and pomacentrids, cichlids and labrids (Perciformes).

In addition, a few other taxa display one of the two features. All clupeomorphs examined revealed ventricular channels, whereas the atherinomorphs display a lateral recess leading to the periphery of the inferior lobe. In the ostariophysans, only the siluroids among the siluriformes revealed one or the other feature. Within the percomorphs, some species of the Gasterosteiformes, Pleuronectiformes and Perciformes (in addition to the above mentioned families of Labroidei) revealed one character or the other.

Discussion

Evolutionary polarity. As Northcutt (1984) has shown, the cladistic method provides a valuable tool for evaluating the evolutionary polarity of neural characters. Based on the phylogenetic relationships of actinopterygian fishes as summarized by Lauder & Liem (1983), a dendrogram of the relevant taxa was constructed, and the two neural features in question were plotted thereon (Fig. 4). From the phylogenetic distribution of the ventricular, hypothalamic channel-system, several hypotheses can be formulated regarding its emergence within actinopterygian fishes. As it is present in only some clupeocephalans and lacking in all of the outgroups, it is most likely that it developed at this stage of actinopterygian evolution and represents an apomorphic (derived) character for clupeocephalans.

There are two possibilities regarding the clupeocephalans: the features may be plesiomorphic (primitive) for this group and have been repeated-

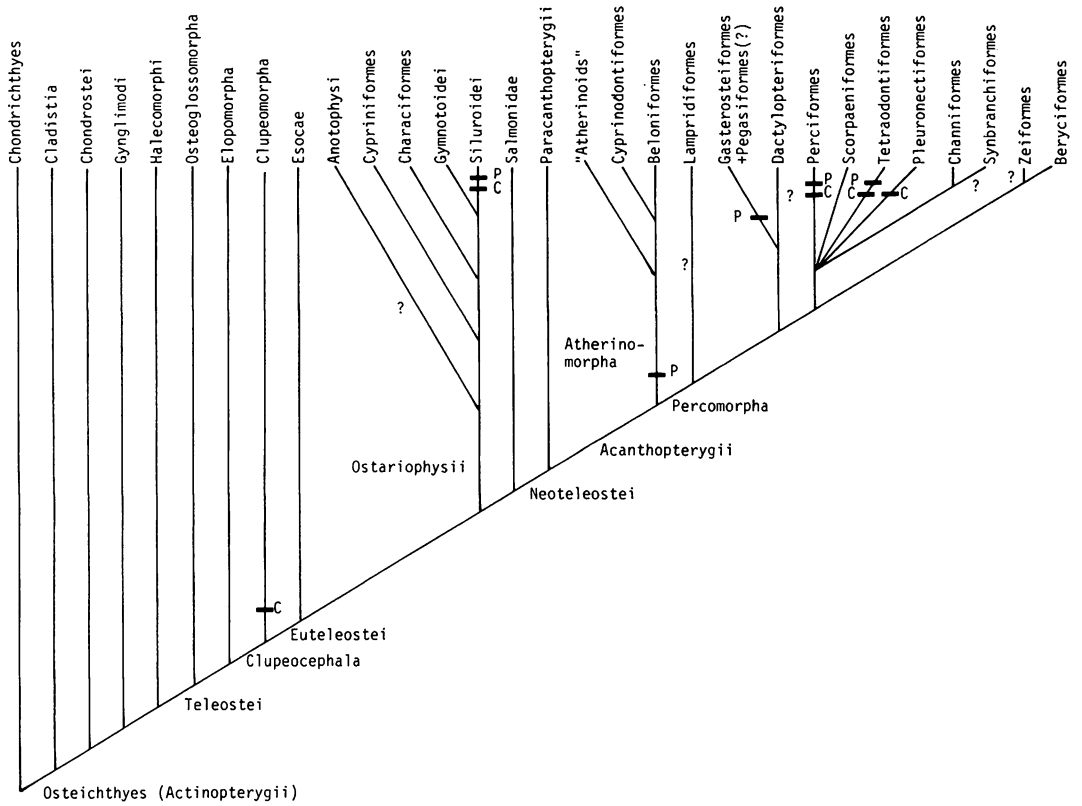

Figure 4. Dendrogram of the phylogenetic relationships of actinopterygian fishes (as summarized by Lauder & Liem 1983), on which is plotted the distribution of the two neural characters comprising the hypothalamic, ventricular channel-system: the existence of ventricular channels leading to the medio-ventral periphery of the inferior lobe (C) and the presence of a lateral recess leading to the medio-ventral periphery of the inferior lobe (P). The phylogenetic distribution indicates that the ventricular, hypothalamic channel-system represents an apomorphic neural character within clupeocephalan fishes. A question mark indicates that no representatives of this group were examined.

ly lost, or they may have arisen several times independently. Their distribution (Fig. 4) indicates that they probably evolved at least three (and possibly seven) times independently – in the clupeomorphs, in the siluriods and (1–5 times) in the acanthopterygians (atherinomorphs and percomorphs). Any hypothesis of plesiomorphy (for P and/or C) at the clupeocephalan or the ostariophysian stage would require at least 13 or 12 transformations, respectively, whereas a hypothesis of parallel apomorphy would require only ten or nine transformations, respectively.

In contrast, the most parsimonious hypothesis of plesiomorphy regarding these characters for acanthopterygians would only require six transformations (plesiomorphy for P in atherinomorphs and gasterosteiforms, but subsequent loss and regain in the remaining percomorphs), whereas a hypothesis of parallel apomorphy would require seven transformations. Within the Percomorpha, however, a minimum of seven transformations would again be required to interpret these characters as plesiomorphies, as opposed to six in the case of apomorphies. Thus the most likely evolutionary scenario for these two characters is that they (either one or both) have evolved six times independently within the clupeocephalans, but that P has originated only once for both atherinomorphs and gasterosteiforms. However, the present interpretation would be strengthened by additional analysis, as some groups of acanthopterygians have not been examined for these characters. The fact that two species of the genus *Lepomis* differ in the presence of C indicates that an analysis on a lower systematical level (in this case within the Perciformes) would even enlarge the number of possible evolutionary events for these features.

Based on the above interpretation, the fully developed channel-system can be viewed as a synapomorphic (shared derived) character uniting the pomacentrids, cichlids and labrids of the suborder Labroidei; the presence of a lateral recess opening to the outside of the brain can even be recognized as a synapomorphy for all of the four families of this suborder, including the embiotocids.

Biological role. In vertebrates, the periventricular nuclear areas bordering the third ventricle and the central canal of the spinal cord differ from the remaining periventricular grey of the brain in that they display numerous cerebro-spinal-fluid (CSF)-contacting neurons. In actinopterygian fishes the hypothalamic nuclei containing CSF-contacting neurons include the neurosecretory nuclei, which are known to project to the pituitary (Vigh-Teichmann *et al.* 1970*a*, 1976, Haider & Sathyanesan 1972, Vigh & Vigh-Teichmann 1973, Holmes & Ball 1974, Moitra & Medya 1980), as well as other nuclei that are not part of the hypothalamo-hypophyseal complex (Vigh & Vigh-Teichmann 1973). Among the latter, the periventricular nucleus of the lateral recess of the inferior lobe is known to possess CSF-contacting neurons (Evan *et al.* 1976). Both secretory and sensory functions, with respect to the CSF, have been ascribed to these specialized ventricular neurons (Vigh-Teichmann *et al.* 1970*a*, 1976, Vigh & Vigh-Teichmann 1973, Parent 1979, Vigh *et al.* 1983).

The lateral recess of the inferior lobe and its periventricular nucleus are, therefore, almost certainly involved in transmitting information between the CSF and the central nervous system (CNS). The development of a more elaborate system in that region, such as the channel-system described, would theoretically allow new pathways for transmission among the CSF, the CNS and the bloodstream and is consistent with the known data described above.

Behavioral data for teleosts (Demski & Knigge 1971, Demski 1973, 1981, 1983, Peter 1979) indicates that the inferior lobes are involved in the neural circuitry mediating motor responses normally observed in feeding and aggression. Part of the neuronal basis for these phenomena has been revealed in *Cyprinus carpio* Linnaeus (Luiten & Van der Pers 1977), where cells of the periventricular nucleus and nucleus diffusus of the inferior lobe (terminology after Braford & Northcutt 1983), as well as those of the preglomerular nucleus, project to the trigeminal, whereas only neurons of nucleus diffusus and the preglomerular nucleus send axons to the facial motor nucleus.

In the crucian carp, *Carassius carassius* Linnaeus, tertiary gustatory fibers have been shown to project to the nucleus diffusus of the inferior lobe and to nucleus 'glomerulosus' (Morita *et al.* 1980). Secondary and tertiary gustatory fibers to nucleus 'glomerulosus' in the bullhead catfish, *Ictalurus nebulosos* Lesueur, have also been reported (Finger 1978, 1983).

Based on these anatomical and behavioral results and some additional physiological evidence, a region dorsal to the rostral beginning of the lateral recess was designated by Demski (1981) the 'hypothalamic feeding area' (HFA). Demski also suggested a model of the underlying neuronal circuitry, in which olfactory and gustatory input dominates the possible biological role of the HFA.

This model may very well be adequate for cyprinids and silurids. It should, however, be

noted that part of the behavioral evidence on which the model is based derives from experiments on perciforms such as centrarchids and cichlids. The neuroanatomy of the hypothalamus in perciforms and tetraodontiforms differs drastically from that in cyprinids and silurids. The latter lack a conspicuous nucleus glomerulosus, which is present in perciform and tetraodontiform teleosts and is known to receive projections from visually related nuclei in *Navodon modestus* Günther. In turn, the nucleus glomerulosus is interconnected by a huge fiber tract with the inferior lobe (Sakamoto & Ito 1982). Perciforms and tetraodontiforms thus possess a neuronal circuitry in that region that is strongly involved in processing visual information and is very different from that in cyprinids and silurids.

The perciform (labrids, pomacentrids and cichlids) and tetraodontiform (balistids) fishes that were shown by the present study to possess a fully developed channel-system in the inferior lobes are also highly dependent on visual clues. Furthermore, they are characterized by complex social systems (Fricke 1974, 1979, 1980, 1983, Fricke & Holzberg 1974, Robertson 1972, Coates 1982, Ross *et al.* 1983), in which marked plasticity of growth, social function and, in some cases, even sex occurs (Sale 1977). In is therefore suggested that the hypothalamic, ventricular channel-system in these cases serves as part of a hormone-producing system (of unknown function) that acts as a bridge between humoral and neural processes.

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